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THE OSSICULA AUDITUS AND MAMMALIAN ANCESTRY.

J. S. KINGSLEY AND W. H. RUDDICK.

THE various students who have investigated the mammalian ear-bones have arrived at the most diverse views as to their homologies, and it was with the idea of satisfying ourselves which of the several accounts of these structures was correct that we began our studies. As we progressed, however, it became apparent that these ossicles threw no little light upon the broader question of the origin of the mammalia. In our final paper we will give full details of all of our observations, as well as a discussion of the results of other students. The present paper states our views of the homologies of these ossicles in a brief manner and shows the bearings which these have upon the problem of mammalian descent. The material which we have studied has been embryos and larvæ of Amphiuma, Pipa, Ichthyophis, Sceleporus, rat, and pig, and our methods have been largely those of wax reconstruction from sections.

Distinct auditory ossicles occur in no fish-like form, but from urodeles to man, in one shape or another, they are present in all forms. In urodeles there is a large fenestra ovalis in the outer wall of the otic capsule, and in this, connected to its margin by membrane, is a cartilaginous plate which is usually called the stapes. It is unnecessary for our present purpose to consider whether this element is formed from the otic capsule, or is the homologue of the hyomandibular of the fishes, or, again, is an independent structure. In most urodeles this stapes is attached to other structures by ligaments alone, but in Amphiuma as well as in Plethodon (*teste* Winslow) and in all Cæcilians which have been studied, the stapes articulates directly with a stapedial process which is given off from the posterior side of the quadrate. At first this quadrate is free from the cranium, and is connected only with the slender Meckelian cartilage of the lower jaw. A little later the quadrate extends to and fuses with the otic capsule a little above and in front of the fenestra ovalis. This we may term the urodele type of auditory ossicles, although it is a question as to how far they serve as a sound-transmitting apparatus, the tympanum being entirely absent in the urodeles. These features, then, are the possession of a quadrate which acts as a suspensor of Meckel's cartilage, and at the same time articulates with the stapes. It may be noted, in passing, that in the Cæcilians the stapes is perforated, much as in mammals, for the passage of the stapedial artery, a feature which adds to the probability that this element is homologous throughout the pentadactyle vertebrates.[1]

Of the anura we have studied Pipa, and our results here are much like those of Gaupp upon Rana. In both of these genera the essential features from our present standpoint show no affinities with the urodeles, but resemble rather those of the sauropsida, and hence a description of the relations in a lizard will answer present purposes.

In Sceleporus, which we take as the sauropsidan type, and in which we have studied several stages of the conducting apparatus, the auditory chain consists of a stapes lying in a fenestra ovalis, and, connected with this, a columella consisting of at first a cartilage rod extending horizontally outward into the tympanic membrane. When first differentiated, the shaft of this columella lies in the mesenchyma posterior to the entodermal diverticulum, the distal end of which expands later to form the tympanic cavity. In other words, *the columella is postspiracular.* Another point of considerable importance, and one which has been neglected by most previous students of the auditory ossicles, is the relation of the stapedo-columellar tract to the adjacent nerves. The facial nerve, after leaving the cranium, passes backward just outside the otic capsule, running above the stapedo-columellar shaft. At the most posterior point of its excursion the facialis gives off a nerve, the chorda tympani, which runs forward *above* the shaft of the columella and on the medial side of the quadrate, to extend into the lower jaw, together with the mandibular branch of the trigeminal nerve. With further development the columella seemingly invades the tympanic cavity. In reality the cavity in its expansion extends around the rod, which, however, remains connected with the posterior tympanic wall by means of a fold of the tympanic epithelium and the enclosed mesenchyma. The quadrate, contrary to what obtains in the urodeles, does not articulate with the stapes, nor is it connected, except by ligament, with the sound-conducting apparatus. Its sole function is that of a suspensor of the lower jaw. The sauropsidan type, then, may be characterized as consisting of a stapes and a columella which form the auditory chain, the columellar shaft being post-trematic in origin, while the quadrate is outside of and apart from the sound-conducting apparatus.

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[1] In spite of this similarity between the auditory chains of Cæcilians and Amphiuma, we do not agree with Cope that the Cæcilians have descended from Amphiuma, nor with the view of the Sarasins that Amphiuma is a neotænic gymnophione. The senior author hopes to present his views upon these points at an early date.

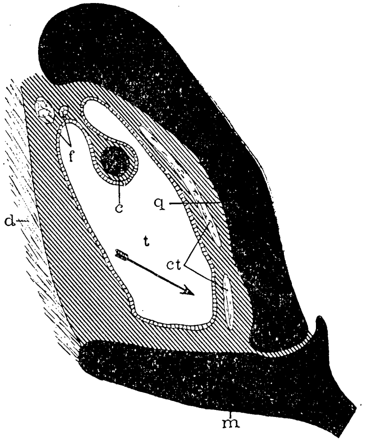

Fig. 1. — Section through the tympanic region of an embryo of *Sceleporus undulatus*, showing the columella, *c*, entering the tympanic cavity from behind; the arrow points towards the tip of the snout, the cartilages are black. *d*, digastric muscle; *ct*, chorda tympani; *f*, facial nerve; *m*, head of Meckel's cartilage; *q*, quadrate; *t*, tympanic cavity.

All other questions regarding this apparatus in the sauropsida must be ignored here — the question of the homologies of the stapes, the relations of both stapes and columella to the hyoid and hyomandibular, etc., as well as discussions of muscles; we can only call attention to the fact that there is some evidence to show that that portion of the columella which lies within the tympanic membrane may possibly be homologous with the manubrium of the mammalian malleus, to be described below.

In speaking of the auditory ossicles of the mammals, it will be necessary to go into more detail, since, while the different features of development have been described several times, there is great diversity of opinion as to the homologies of the parts concerned.

In the pig the ossicula auditus and related parts can first be made out in embryos measuring about eighteen millimeters in total length, and sagittal sections give the clearest pictures. In embryos of this size the otic capsule has not begun to differentiate, the utriculus, sacculus, and semicircular canals being imbedded in a homogeneous matrix of mesenchyme, which nowhere shows that concentration of nuclei so characteristic of procartilage formation. The stapes, on the other hand, is well outlined as a mass of procartilage formed around the stapedial artery, the mass having the form of a ring rather than the stirrup shape of the adult. Ventral to the stapes is the Eustachian cleft, which as yet shows no differentiation into tympanic cavity and tube. This cleft extends outward for some distance above and parallel to the inner end of the external

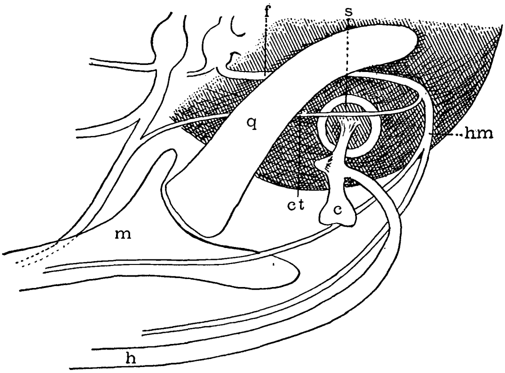

FIG. 2. — Diagram of otic region in Sceleporus embryo: *c*, columella; *ct*, chorda tympani; *f*, facial nerve; *h*, hyoid; *hm*, hyomandibular nerve; *m*, head of Meckel's cartilage; *q*, quadrate; *s*, stapes in foramen orale; the otic capsule shaded.

meatus. The tissue between these two tubes is to form the tympanic membrane, its plane being now nearly horizontal instead of oblique, as in the adult. In this membrane is formed a rod of procartilage entirely unconnected with any other skeletal structure, the Anlage of the manubrium mallei. In front this procartilage gradually shades off into the looser mesenchyme between it and the mandibular arch, while behind it is very sharply delimited from the undifferentiated tissue lying between it and the hyoid.

In front of the Eustachian cleft and external meatus is another mass of procartilage, the anlage of the mandibular arch. At first it consists of a continuous stroma, which extends proximally and dorsally to a point just in front of the stapes, distally into the lower jaw. This procartilage rod is not equally dense throughout, but at the level of the future tympanic membrane the nuclei are less crowded than they are above and below. This indicates a division which later becomes more marked, separating a proximal element, the incus, from a more distal portion which will give rise later to a proximal body of the malleus and its processus longus and a more distal rod of cartilage which extends into the lower jaw. So far, with the exception of the separate origin of the manubrium of the malleus, all who have approached the problem of the mammalian ear-bones from the developmental standpoint are in agreement. The differences of opinion are regarding the nature of the incudal element.

In the pig embryo, twenty millimeters long, several changes have been introduced. Chondrification of the otic capsule is well advanced, the foramen ovalis being formed around the base of the stapes in such a way that it lies within the opening. In the stapes itself the process of chondrification has set in, while outside the junction of its crura arises a short process which articulates with a stapedial process of the incus. The body of the incus is now an elongate plate with rounded extremities, the whole occupying a vertical position. The dorsal end extends up to, and may be said to articulate with a depression in the outer wall of the otic capsule, just above and outside the foramen ovale. Below, the stapes also articulates with the body of the malleus. The stapedial process of the incus is a slender rod, smaller than the body, which extends backwards and slightly downwards to the stapes. From the body of the malleus a strand of cartilage has extended backwards and has fused with the manubrial cartilage noticed above, the whole forming the manubrium of the adult. Distally, the mallear cartilage is still continuous with the rest of Meckel's cartilage, extending into the lower jaw.

At this stage we can recognize clearly the three[1] ossicles and their processes of the adult ear. So far they all lie outside of, and, so far as incus and body of the malleus are concerned, in front of the tympanum; they are prespiracular. Hence it follows, as certainly as any morphological conclusion can be drawn, that they cannot be homologized with the columella and its derivatives in the sauropsida, as has been attempted by Albrecht, Dollo, and others. This lack of homology is still further emphasized by the course of the chorda tympani, which in its course passes *below* the articulation of incus and stapes, and then forward on the inner or medial side of the incus to the fifth nerve. It may, however, be possible that the manubrial portion of the malleus is homologous with the distal portion of the columella.

The question now comes up for decision, What are the homologues of incus and malleus in the lower vertebrates? All recent students are in agreement that the body of the malleus is derived from Meckel's cartilage, for it retains its connection with the cartilage of the lower jaw for some time; but whether it is the articulare of non-mammalian groups can only be decided later, after a discussion of the incus. Concerning this latter bone two views are held at present, for no recent student has attempted to recognize in it the hyomandibular. According to one view the incus is the quadrate, while according to the other it arises from the proximal end of Meckel's cartilage, while the quadrate, according to this same view, has fused with or has become lost in the squamosal region of the mammalian skull.

The greatest objection which has been advanced to the first of these homologies — the incus-quadrate homology — is that it must necessarily follow that the articulation of the lower jaw with the cranium in the mammals cannot be homologous with the articulation in the lower vertebrates, and that it is difficult to imagine this transfer of functions from one point to another. The weight of this objection we admit, but we shall endeavor to show a little later that no matter what view one takes of the fate of the quadrate in the mammals, there is this same problem of the formation of a new articulation to be met, for it is impossible, upon any basis, to homologize the articulation of the lower jaw in the mammals and the non-mammalian groups.

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[1] The os-obiculare or lentiforme occurring between the incus and stapes is a later structure without morphological significance.

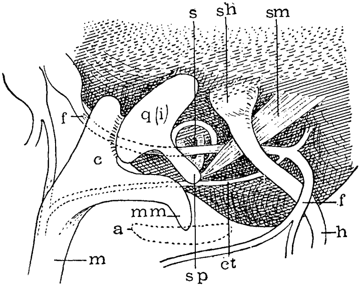

Fig. 3. — Diagram of otic region in pig embryo: *a*, position of external meatus; *c*, body of malleus; *ct*, chorda tympani; *f*, facial nerve; *h*, hyoid; *m*, Meckel's cartilage (processus longus); *mm*, manubrium mallei; *q* (*i*), quadrate (incus); *s*, stapes; *sh*, styloid process of hyoid; *sm*, stapedial muscle; *sp*, stapedial process of quadrate.

In all ichthyopsida and sauropsida the articulation of the lower jaw with the cranium is in reality an articulation between the quadrate and Meckel's cartilage, and even when it becomes an osseous articulation it is an ossification of the cartilages which affords the articular surfaces. In the mammals, on the other hand, Meckel's cartilage does not approach in any way to the glenoid fossa. The mandible forms around the distal portion of Meckel's cartilage as a membrane bone, and its ascending ramus grows away from the cartilage towards the glenoid fossa. So it is evident that the mandibular part of the articulation in the mammals is not formed by the Meckel's cartilage. How about the fusion of the quadrate in the squamosal, as maintained by Peters, Albrecht, and Cope? Development shows us not the slightest trace of cartilage in the region of the squamosal;

there is nothing but membrane bone. Besides, the proper position for the quadrate is at the proximal end of Meckel's cartilage. But Meckel's cartilage extends far back of the glenoid fossa, and one cannot readily imagine any reason for the transfer of the quadrate from one position to another. In a word, it is as incumbent upon those who claim that the quadrate has been lost in the squamosal region as upon those who recognize the quadrate in the incus, to explain the formation of a new articulation in the mammals.

An easily accessible figure will illustrate these points: Fig. 254 on p. 467 of Bell's translation of Gegenbaur's *Comparative Anatomy.* If the articulation of the lower jaw of mammals be homologous with that of lower vertebrates, then Meckel's cartilage (*p*) should run up into the glenoid fossa. If the incus (*i*) be the proximal end of Meckel's cartilage, then the quadrate should be sought between it and the cranial wall immediately adjacent. It is difficult to imagine how the quadrate could be translated from the point crossed by the "leader" from *i* to a point in the glenoid fossa crossed by the "leader" from *p*.

If, on the other hand, we suppose that the proximal end of Meckel's cartilage be represented by the body of the malleus, then the incus is in just the proper position for the quadrate; and the proportionally large size of this element in its earlier stages shows that it must have been of large size in the ancestral form. Then, again, in the embryo this incus acts as a true suspensorium of the lower jaw, while its connection with the stapes is of secondary size. In short, it fulfills every condition demanded of a quadrate in position and relation to other parts, and we doubt if its nature would have been questioned were it not for the hypothesis that the mammals had descended from the theromorphs in which the squamosal as well as the quadrate enters into the formation of the articular surface for the lower jaw.

One objection to the view that the incus is the quadrate is based upon the fact that it does not appear from the first as a discrete element, but is differentiated from a continuous stroma. This objection loses much of its force when we consider that both Meckel's cartilage and the palatoquadrate of the elasmobranchs arise from a continuous cord of cells, and only with the process of chondrification does differentiation occur. In the digits the separate phalanges are likewise developed from a continuous mass of procartilage cells. In the light of all the evidence we feel impelled to agree with the majority of the embryological students who have studied the question and to regard the incus as the quadrate.

It appears to us that the relations of these ear-bones throw no little light upon the question of the origin of the mammals, or at least of the so-called higher mammals, since it is not beyond question that the mammals are a monophyletic group. For many years it was the general supposition that the mammals have descended from the Amphibia. Then came the discovery of the meroblastic ova of the monotremes, and the almost simultaneous announcement of the recognition of mammalian features in the theromorphous reptiles. Then for several years the prevailing view was that the mammals must have had a reptilian ancestry; but the pendulum began to swing backwards. The difficulty of the double occipital condyle remained. Hubrecht has pointed out the difficulty of deriving the mammalian ovum, with its peculiarities of segmentation, gastrulation, and especially its fœtal envelopes, from the sauropsidan type, while these can readily be evolved from the amphibian egg. Maurer has shown that it is impossible to compare the hair, so characteristic of mammals, with any known structure in reptiles; while, on the other hand, he has pointed out the close resemblances even in structural details between hair and the epidermal sense organs of the Amphibia.

Now, when we consider the ossicula auditus we see the impossibility of deriving those of the mammals from those of the reptiles. As we have shown, the shaft of the columella in the reptiles is postspiracular and is below the chorda tympani, while the incus and the body of the malleus are prespiracular and are above and outside of the chorda tympani. On the other hand, the mammalian ear-bones with all their peculiar features (the manubrium of the malleus excepted) are derivable from those of some urodele-like form. In the urodeles, as in mammals, we find an articulation of stapes with quadrate, while in the reptiles no such articulation occurs.

Another fact which has a bearing upon the question of the origin of the mammalia has not, so far as we are aware, been referred to. In the urodeles[1] there develop a pair of thoracic ducts, one duct emptying into the venous system on the right side, the other into the left, near the heart. Of these ducts, the left is from the first the larger, while a little later the right completely disappears, leaving the left as the functional duct of the adult. This disparity in size from the first would show that this left-sided condition had persisted for a long time. In the mammals, as is well known, the left thoracic duct alone is functional, while in all sauropsida it is the right that persists. It is, therefore, impossible to derive the mammalian conditions from those found in any existing reptile, but of course one cannot say but what the earlier reptiles had this part of the lymphatic system paired. However, the conditions in the urodeles are suggestive.

We would not be understood to derive the mammals from any true urodele stock, but from some ancestor not widely removed from them. The urodeles, as we know them to-day, are a degenerate group, possibly descendants from terrestrial forms, and the lowest of the group, like Necturus, etc., have departed most widely from the ancestral type. The urodeles have lost many cranial bones; they have reduced the ribs, they have lost entodermal gills and gained those of ectodermal origin; they have lost the Eustachian tube, but they have retained many features which make them extremely interesting in connection with all phylogenetic speculations.

If, now, we advocate the amphibian origin of the mammals, we must consider the arguments of those who would derive them from the theromorphous reptiles. The chief of these are as follows:

In certain theromorphs, as in most mammals, there is a heterodont dentition; incisors, canines, and molars being differentiated. This, however, is not conclusive, since a heterodont dentition is not extremely rare in the non-mammalian vertebrates, which are certainly far removed from the mammalian line. On the other hand, the theromorpha have single-rooted teeth throughout, while certain of the dinosaurs have them with two roots. Heterodont dentition may easily be explained by parallel development from similar conditions.

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[1] For our knowledge of the development of the lymphatic system of the urodeles we are largely indebted to the unpublished investigations of Dr. F. D. Lambert.

In the theromorphs, as in the higher mammals, the coracoid is united to the scapula. This point is as favorable to the amphibian as to the theromorphous ancestry, since a similar state of affairs occurs in certain existing urodeles.

In theromorphs, as in mammals, there are bicipital ribs, one head articulating with the neural arch (diapophysis), the other with centrum or intercentrum. Here again the urodeles will fill the bill.

In the theromorphs, as in many mammals, there is an entopicondylar foramen in the humerus. This seems a feature of minor importance, since it is lacking in many mammals, while it is developed in some forms (*e.g.*, Hatteria) which cannot have had a theromorphous ancestry.

In the theromorpha, ischium and pubis fuse to form an innominate bone. This feature also occurs in certain urodeles as well as in some other reptiles.

In certain theromorphs (Clepsydrops) there is a differentiation of calcaneum and astragalus, recalling the relations in the mammals. Unfortunately, almost nothing is known of the foot structure in other theromorphs, and the resemblances pointed out in Clepsydrops are not conclusive. In all other sauropsids there is a strong tendency towards the development of an intratarsal ankle joint. Certainly the mammalian tarsus could have been derived directly from that of the Amphibia instead of indirectly through the theromorphs.

There is one serious objection to the theromorphous ancestry of the mammals upon which sufficient weight has not been placed. This view assumes that the suspension of the lower jaw in the theromorphs is, at least in part, homologous with that in the mammals. It assumes that the glenoid fossa of the latter has arisen by the squamosal of the reptile usurping the functions of the quadrate. But here lies a difficulty other than that presented on a preceding page. If this assumption be true, the articular head of the mammalian lower jaw should represent the articulare, while between this and the tip of the jaw, several bones — angulare, splenial, dentary — should occur. In fact, the lower jaw in every mammal, so far as known, ossifies as a single membrane bone, which we prefer to regard, until better evidence is forthcoming, as the dentary of the lower vertebrates. The articulare we recognize in the body of the malleus, while since a new fulcrum of the lower jaw has been formed, the other bones, angulare, supra-angulare, splenial, etc., having no longer cause for existence, have disappeared without leaving a trace behind. Their proper position would be around that portion of Meckel's cartilage which for a while persists between the malleus and the osseous lower jaw.

In examining the shape, relations, etc., of the manubrium, which, as was noticed above, arises separately from the rest of the malleus, one can hardly fail to be struck with its resemblance to a somewhat reduced visceral arch. This resemblance is the more interesting since the cartilage appears in the very place where, according to several students of the problem of the segmentation of the vertebrate head (Dohrn, van Wijhe, Beard, Locy, Neal, etc.), a segment has apparently almost entirely disappeared from the vertebrate head. Whether this and the distal cartilage of the reptilian columella be the visceral arch of the missing segment, and whether the Eustachian tube really represents two confluent gill slits, we do not at present care to discuss.